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Evidence that no liquid equilibrium process is involved in the comb building of honey bees (*Apis Mellifera*)

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Abstract:

According to Pirk et al. (2004), honeybees first build free standing cylindrical cells which are then transformed to hexagonal cross-section by wax-flow in a kind of self-organization. We show that there is no self-organization of the wax. Bees cannot form juxtaposed wax tubes which are in contact to each other. They would have to produce temperatures close to the melting point in order to accomplish flow of the wax in a time which is meaningfully short for honeycomb construction. The cells would collapse at this temperature. The form of the comb-cells adjacent to the walls of the nest cannot stem from circular tubes. From this it is clear that bees build their honeycomb in a direct and holistic way. They begin and continue building at the edge of the mid-wall. The combination of the following two principles inevitably generates the hexagonal cross-section of the cells: (1) the hexagonal close packing of the cells and (2) a common wall between all adjacent cells. This results in an economic use of space and material. The mid-wall can be considered as assembled of parts of Plateau's minimum plane of the regular tetrahedron and is built with minimum consumption of wax as are the cells.

Zusammenfassung

Nach Pirk et al. (2004) bauen Honigbienen beim Wabenbau zunächst frei stehende zylindrische Zellen, die dann durch das Fließen des Wachses in einer Art Selbstorganisation in den hexagonalen Querschnitt umgeformt werden. Wir zeigen, dass Selbstorganisation des Wachses nicht auftritt. Bienen können keine dicht nebeneinander liegenden, sich berührenden Wachsröhren bauen. Um ein Fließen des Wachses in einer für den Wabenbau sinnvoll kurzen Zeit zu bewerkstelligen, müssten sie Temperaturen knapp

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unterhalb des Schmelzpunktes erzeugen. Bei dieser Temperatur würden die Zellen kollabieren. Die Form der Zellen im Kontakt mit den Wänden der Nisthöhle kann nicht aus runden Röhren entstanden sein. Das macht klar, dass Bienen ihre Waben direkt und in einer ganzheitlichen Weise bauen. Sie beginnen den Bau mit der Mittelwand und bauen an deren Rand sukzessive weiter. Die Kombination folgender zwei Prinzipien erzeugt zwangsläufig den hexagonalen Querschnitt der Zellen: (1) die hexagonal dichteste Packung der Zellen und (2) eine gemeinsame Wand zwischen allen benachbarten Zellen. Das führt zu einer ökonomischen Nutzung von Raum und Material. Die Mittelwand kann als aus Teilen der Plateau'schen Minimalfläche des regulären Tetraeders zusammengesetzt betrachtet werden.

Keywords: honeycomb/comb building/hexagonal cells/mid-wall/minimum consumption of wax/direct building of hexagonal cells

1 Introduction

Recently the age-old question has been increasingly discussed of how honeybees build their combs with the regularly arranged hexagonal cells. These combs are admired of their well-engineered architecture and their astonishing multi-functionality. We will not discuss all the many questions related to the building of such a complex honeycomb in a combined action of hundreds of individuals but we will confine ourselves to just one: “Do the bees build circular precursor structures of the comb cells which are then transformed into hexagonal cells, or do they build the hexagonal cells directly?” This question was raised in the past by many researchers – amongst them Charles Darwin – as sketched by Oldroyd and Pratt (2015). The question was taken as hypothesis by Pirk et al. (2004) and has been spread through the literature for some years (Karihaloo et al., 2013, Dietemann et al., 2011, Tautz, 2012, Tautz and Steen, 2017). Pirk et al. (2004) present their hypothesis with a question mark in the title, but this questioning nature of the title is not found in the article any more. Their hypotheses read:

1. Honeybees build cells not as hexagonal prisms, but as cylinders.
2. The cylindrical cells are transformed into cells with hexagonal cross-section by thermoplastic flow of the wax in a self-organising process upon heating of the wax by the bees.
3. The cell bottom has a hemispherical shape and is not formed by three rhomboids. The apparent rhomboids are an optical illusion.

Despite an earlier rebutting publication (Bauer and Bienefeld, 2013), these hypotheses are still repeated in the literature (Tautz, 2015) and in many posts on the internet. This is why we try to contribute to the discussion with our additional findings in order to resolve the dispute.

In the following we use “cylinder hypothesis” as an alias term comprising the points of Pirk et al. (2004) mentioned above. The cylinder hypothesis was probably accepted so uncritically because one can deform cylindrical model-tube bundles in a way that the cross-section of the tubes is converted into a hexagonal form. But the effective mechanisms are different in these cases and cannot be applied to honeycombs. Also the realization of honeycomb structures in ceramics (Melcher, 2008) does not apply to the formation of hexagonal cells in honeycombs. In terms of Camazine et al. (2001), self-organization of the wax does not take place since the bees would already impose an external ordering influence on the system by grouping of the cylinders in the hexagonal close-packed pattern.

Pirk et al. (2004) created the term “… wax flowing in liquid equilibrium”. We note that “flowing” excludes equilibrium. The authors refer to the famous physicist L. Boltzmann when asserting “… the liquid wax hardens and moves into a more probable state…the result of which is the regular hexagonal pattern”. However, one cannot find any hint about that and “the more probable state of wax” in the cited literature (Boltzmann, 1905). This formulation and citation were used again by Hepburn et al. (2007) in the same way.

Tautz (2012) still postulates a hemispherical cell bottom at least for a couple of days after comb-formation. Hepburn et al. (2007) finally state that the cell bottom has rhombic shape. But their explanation for the formation of the rhombi is not plausible. Bauer and Bienefeld (2013) found no indication of “thermoplastic flow” by observation of comb building. Several authors report on the chemical and physical properties of beeswax but their data do not make thermoplastic flow reasonable (Oelsen and Rademacher, 1979, Buchwald et al., 2008, Kleinhenz, 2008). Calculations which should support the cylinder hypothesis are based on a model with free surfaces in the triple junction of the circular tubes (Karihaloo et al., 2013), which is not the case for honeycombs. The necessary heat transfer from the bees to the wax is questionable (Mazzucco and Mazzucco, 2007, Dietemann et al., 2011). Oldroyd and Pratt (2015) doubt the cylinder hypothesis because the temperature generated by the bees is insufficient to melt the wax. They agree with Bauer and Bienefeld (2013) that bees develop cells actively rather than forming a passive matrix around which wax flows. However, these papers do not seem sufficient to correct the cylinder hypothesis in the eyes of a large public.

When discussing the formation of the hexagonal shape of cells, the three-dimensional structure of the comb is often neglected. The need to think in three dimensions is emphasized already by Fejes Tóth (1964), Weaire and Phelan (1994) and Räz (2013).

The cylinder hypothesis suggests that thermoplastic building material is a prerequisite for the formation of a uniform array of hexagonal cells. The combs of wasps and hornets prove that this is not the case.

Here we show that one cannot follow the cylinder hypothesis. Moreover, we will try to make a large part of the honeycomb construction intelligible.

This paper is structured as follows. We point out in 3.1 the importance of the cell bottom (mid-wall) for the comb structure and its amazing construction. In 3.2 we are dealing with a number of aspects of the cylinder hypothesis which are unrealistic for comb building and we oppose facts based on our own observations. In 3.3 we argue from the hexagonal cells of wasps and hornets that flowable material is not essential for the construction of hexagonal cells and we present in 4 our own arguments and considerations on honeycomb construction on the basis of our own observations and the literature.

2 Materials and Methods

Samples of honeycombs (partly freshly built) were taken from the beehive to demonstrate certain features of building and the building process (Fig. 1, 4, 6).

Wax samples were prepared with razor blades and needles under a binocular microscope (Zeiss). We used only virgin wax, e.g. wax scales or just built comb samples. All photos were taken with digital cameras partly under artificial illumination.

Warming of wax scales was performed over about six hours in several steps from 40 °C to 55 °C in a vessel dipped in a thermostat (stirring thermostat IKA HS7 C-LIKED with IKA ETS-DS sensor). Just built pieces of comb were stored for three hours at a temperature of 55.5 °C in an incubator INCU Line with officially calibrated temperature sensor.

The hornet comb was provided by an expert on wasps and hornets. The hexagons on the back of this comb were sketched using Microsoft PowerPoint (Fig. 8b)

3 Results and discussions

3.1 Construction of the cell bottom

Honeycomb construction by the bees always happens holistically with mid-wall and cells. This can be observed in Fig. 1 on a piece of honeycomb under construction where different stages of comb-building can be seen, beginning with mid-wall and short incomplete cells and almost finished deep cells. Bottomless cells have never been observed even in the earliest stage of cell construction. So the bees first have to set up the bottom to be able to establish a cell on it (Fig. 1). Fig. 1 proves by the rare case of a honeycomb developed only on one side that the rhombi are set up first during its construction. One can see that comb building proceeds by forming new rhombi at the rim of the comb and thus the bottoms of the cells on both sides of the comb are produced in a single work cycle. With a vaulted layer of wax serving as foundation, with the minimum amount of work and without energy-intensive secondary processes, a stable honeycomb with maximum capacity evolves. In case of Fig. 1 we assume that lack of space was the reason for the bees to build cells only on one side. What would the bees have built on this empty side if the comb were given back to the hive with enough space for building? They surely would not have constructed circular tubes, but cells with hexagonal cross-section! This would be the well known behaviour observed with the artificial mid-walls provided by the beekeeper. The above observations show that the cylinder hypothesis is not consistent with the real construction of mid-wall and cells.

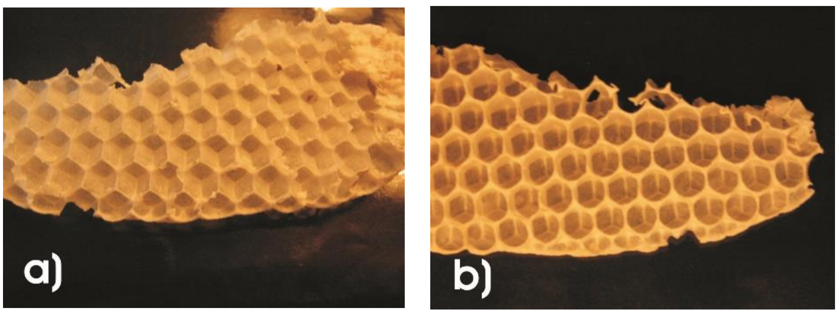

Fig. 1 Half-sided built-up natural honeycomb. a) On this side of the comb no cells have been erected. Thus the rhombic structure of the mid-wall can be seen: three rhombi form the bottom of a cell.
b) Opposite side with cells. The construction of the mid-wall is continued at the lower edge. The 5 mm deep cells in the lower row, as well as the 10 mm deep ones three rows above, are all hexagonal. Particularly in the lowest cell-row the cells are strongly bevelled to the edge (different illumination of the sides)

Pirk et al. (2004) claimed that the cell bottom is of hemispherical shape. This is a contradiction to the literature and everybody's evidence. Their experimental procedure using a polyester resin for moulding the cells seems problematic since the lipophilic casting material can migrate into the beeswax, changing its properties. Hepburn et al. (2007) revised their statements of hemispherically shaped cell bottoms and acknowledged that the bottom of the honeycomb cells is built up with rhombi. However, they still postulate that the rhombi form by themselves "exactly like soap bubbles". This presupposes that the bees initially built a differently shaped cell bottom which ensures the right offset of the cells on both sides of the honeycomb in order to match to the rhombi formed later. This is very unlikely because it is the rhombic form of the cell bottom which is coupled with the displacement of the back-to-back hexagonal cells. We assume that the bees build both the cell bottom and the hexagonal cells in a contiguous way without intermediate steps. The soap-bubble analogy is untenable, because there are no bubble-like intermediate stages in the honeycomb construction. The "formation by itself" is not possible for the non-planar cell bottom. However, one can look at the rhombi in the image of the Plateau's minimum plane of a regular tetrahedron (Fig. 2).

Fig. 2 Minimum plane of the regular tetrahedron; picture from Walser (2011)

The minimal surface is formed by six isosceles triangles whose flat surfaces intersect at angles of 120°. The obtuse angled tips of the triangles meet in the centre of the tetrahedron. Here their sides enclose an angle of 109° 28′ 26′′. This corresponds to the obtuse angle of the rhombi forming the mid-wall. The sides of the tetrahedron plane considered correspond to the long diagonal of the rhombi. Adding together those sections of the minimal surface (formed from the blue, red and olive triangles in Fig. 2) with alternating convex and concave orientation, one gets the structure of the mid-wall (Fig. 3). This approach, not found in the literature up to now, is a confirmation of the principle of minimum wax consumption not only for the cells (Hales, 2001) but also for the cell bottom which gets an extraordinary mechanical strength due to its vaulted structure.

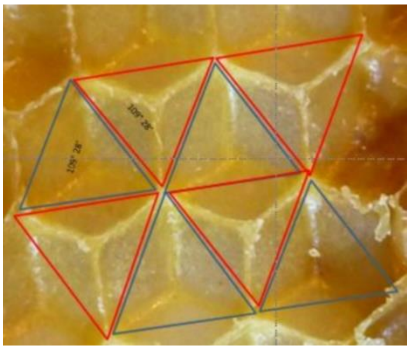

Fig. 3 By alternately joining together concave (blue) and convex (red) sections of the Plateau's minimum plane of the regular tetrahedron, one gets the structure of the mid-wall of a honeycomb

A "liquid equilibrium process" would not lead to the rhombic structure of the mid-wall, since the surface energy of a flat sheet of beeswax would be lower. The surface area of the three rhombi is about 22 % greater than the surface area of a flat bottom, so the latter would be the "energetically more probable state". The "liquid equilibrium process" would never by itself produce a cell bottom made up by rhombi.

3.2 Construction of the cell walls and the "melting" of wax by the bees

3.2.1 Self-organization of the wax is an illusion

Pirk et al. (2004) write: "When heated by the bees, the viscosity of the wax will decrease and the surface tension of the wax will cause the cylindrical tubes to merge … and thus the hexagonal shape of the cells is created". This, indeed, works for a man-made tube-bundle by applying external effects (Melcher, 2008) and works with appropriate assumptions in numerical simulation (Karihaloo et al., 2013). Even if that were similar for cells on honeycombs, one could not speak of "self-organization", because the close-packed arrangement of the cells would have already existed with the close-packed cylindrical tubes created under the external influence of the bees (Camazine et al., 2003). We cannot see the development of a new pattern by the transformation of circular tubes into hexagonal ones but only a modification of the shape of the pattern-forming objects.

3.2.2 The connection to the wall and structural variations on the same honeycomb contradict the cylinder hypothesis

If our honeybees create a new comb on the ceiling of their nesting hole, they start with patches of wax strips, which are subsequently built to form the mid-wall. Perpendicular to it they build on both sides a short series of "half" cells that lie parallel to the ceiling with their longitudinal axis. Their cell bottoms already show an incomplete rhombic structure of the mid-wall and the offset of opposite rows of "half cells" by half a cell diameter (Fig. 4).

Fig. 4 The beginning of the honeycomb structure on a vertical wall with "half cells" in house-shape next to the wall. In the cells attached to the wall one can already recognize in translucent light the vaulted rhombic mid-wall of the completed cells. Even in the very first row the cell-bottom has an incomplete rhombic structure

The conversion of cylindrical tubes into hexagonal cells cannot cope with the observed shape of the cells attached to the wall of the nest. This type of cell could never originate from a free-standing tube adjacent to the solid wall (Fig. 4). When melting, we would expect the spreading of some wax on the solid wall of the nest. This is not observed, and the cell walls standing perpendicular on the nest wall cannot be understood as well in the picture of flowing wax. Since the nest wall shown in Fig. 4 is vertical, thermoplastic flowing wax, following gravity, would never result in cell walls standing perpendicular on it. The cylinder hypothesis is practically disproved by the observed bonding of the comb to the walls of the nest.

In addition to the "normal" vertical pattern, cells in both horizontal and tilted patterns can also sometimes be found on the same honeycomb (Oelsen and Rademacher, 1979). Furthermore bigger drone cells directly adjacent to smaller worker cells can be observed almost on all breeding combs. All of these local variations of the comb structure are not likely to occur as a result of the flowing of wax to a state of liquid equilibrium.

3.2.3 The cylinder hypothesis neglects the third dimension

Both the authors who stand in for the cylinder hypothesis and Karihaloo et al. (2013), who support the cylinder hypothesis with their calculations, consider only the hexagonal cross-section of the cells and not the entire honeycomb with mid-wall and the opposite side of the comb. A real cell, however, has not only a cross-section but also a height.

The surface tension of liquids leads them to take the shape with the lowest surface energy. The cylinder hypothesis is based on this phenomenon. Surface tension driven thermoplastic flow of the beeswax at elevated temperature should cause the claimed outer surfaces at the triple points of the wax cylinders to disappear. However, if a surface tension driven thermoplastic flow were relevant, the cell wall and therefore the whole cell will shrink in height as soon as the wax reaches the onset temperature for thermoplastic flow. This happens because the surface of the cell walls can be reduced in this direction without a force counteracting surface tension. This would also have happened already at incremental steps during the progress of wall building if the bees at that time would produce the temperature required for merging the cylinders. So, if point 1 of the cylinder hypothesis were correct, the bees by warming the wax (point 2) would cause the cylinders to collapse in height. This would make the construction of a cell impossible.

3.2.4 Bees cannot build abutting tubes with wax-free triple junctions

A further objection to the cylinder hypothesis is to ask how the bees can build close to each other freestanding wax-tubes with a wall thickness of about 0.035 mm. It is known that during the cell building process, honeybees mould the wax with the mandibles and add wax portions on the upper rim of the cell. Therefore a gap at least the width of a jaw should remain between the tubes. But wax tubes which do not touch would never flow together.

In areas where three tubular cells would abut, the outer surfaces of the tubes would include wax-free cavities. For drone cells, these cavities would have a diameter of about 1 mm, and should be visible with the naked eye. Since some time is required for heating and flow of the wax (Karihaloo et al., 2013), cylindrical cells should be observable on a honeycomb just under construction. But on such honeycombs, which we took from the hive, neither even rudimentary cylindrical tubes nor wax-free cavities can be found by thorough inspection. This is confirmed by Oldroyd and Pratt (2015).

On the contrary, in naturally built honeycombs we observe cells near the edge with low altitude which already have hexagonal cross-sections (Fig. 1 and Fig. 7). Bevelled cells at the rim of the comb have the appearance of elliptically rounded skew cuts and can give the impression that their cross-section is not hexagonal. Even Karihaloo et al. (2013) report cells with a height of only 0.5 mm that are already hexagonal in shape. They do not report cylindrical cells. Our observation is supported by direct video observation (Bauer and Bienefeld, 2013) showing that neighbouring cells have only one common wall and therefore only internal surfaces. These authors investigated both the building at the edge of the comb and the reconstruction of excised cells.

Even if the transition from round cells and hemispherical bottom to the regular hexagons including the three rhomboids were a continuous process (Tautz J., 2016), one should be able to observe all these forms together with their intermediate states on a honeycomb just under construction. But this is not the case. Moreover, we cannot imagine that bees can afford to waste that much time by first building twice as many thin walls as are finally needed and later fusing them together into thicker walls.

3.2.5 Problems with necessary temperature and time

Another argument against the cylinder hypothesis relates to the warming up of the wax by so-called “heater bees”. Beeswax as a multi-component material contains organic molecules of different chain lengths, branching, and saturation. Measurements of Buchwald et al. (2008) indicate the softening of wax beginning at 40 °C and melting at about 64 °C. However the temperatures in the beehive measured by different authors are too low to cause a flow driven by the small surface tension of the viscous wax in a time relevant for the honeycomb construction.

We made experiments on wax scales and cell walls of a newly built comb to test the significance of surface-tension-driven flow for joining the cylindrical cells at the temperatures reported. Both, wax scales and cells have a large surface to volume ratio. If surface tension would be relevant at temperatures in the beehive, they should change their shape on warming in such a way that their surface becomes smaller. When warming the wax scales over about six hours in several steps from 40 °C to 55 °C no observable change of their shape and size occurred.

Fig. 5 shows a cut-out piece of honeycomb with free-standing cell walls with a large surface area. It was stored for three hours at a temperature of 55.5 °C. Here also we could not recognize any change reducing the surface of the cell walls.

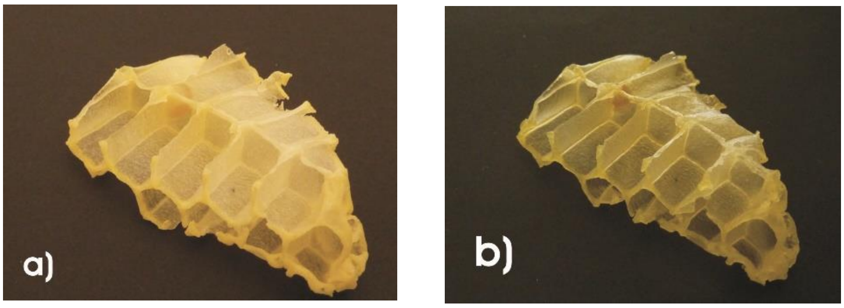

Fig. 5 Honeycomb piece; a) before and b) after the annealing 3 hours at 55.5 °C. No changes are to be recognized (small deformations are due to the handling)

Our simple experiments prove that even at temperatures slightly below the melting point the viscosity of the wax is too high for the surface tension to cause the wax to flow. And this although the viscosity decreases exponentially with increasing temperature, while the surface tension decreases only linearly. This confirms undoubtedly that the surface tension of the wax is irrelevant for honeycomb construction. The conditions necessary for the cylinder hypothesis would evidently be met only under the unreasonable assumption that the wax is not only plastic, but liquid.

Bauer and Bienefeld (2013) also found no indication of “thermoplastic flow”. They measured a temperature around the worker bees between 33.6 °C and 37.6 °C. This is significantly below 40 °C, the reported transition temperature from solid to plastic wax.

We will now discuss the problems with temperature and time that arise if bees were to try to construct a comb, especially a drone-comb, according to the cylinder hypothesis. The cross-section of drone cells is more than 40 % bigger than that of worker cells. In a drone cylinder a bee would therefore not only be surrounded by its thermally insulating hair coat (Mazzucco and Mazzucco, 2007, Dietemann et al., 2011) but also by an insulating layer of air with a heat conductivity σ = 0.02 W/mK (von Böckh, 2006). Also wax with σ = 0.15 W/mK (Kleinhenz, 2008) is a good thermal insulator. To heat the wax to the temperature of 40–45 °C (Pirk et al., 2004, Karihaloo et al., 2013) under these poor heat transfer conditions, the construction bees would have either to spend much time or have to develop a body temperature that is presumably lethal for them.

Apart from that, let us consider the following scenario: a drone cell can only hold one worker bee, but the bee is too small to heat the wall completely. Therefore the heating at the corners of the future hexagon must be performed sequentially. To do so, two other bees, one in each of the cells adjacent to the corner in question, would have to wait and realize that they have to heat at the interface to the central cell at exactly the same time as their colleague in the middle heats at this triple junction. In each case three workers would have to co-ordinate themselves with their heating work. Both this coordination effort and the amount of workers needed are unlikely. On a honeycomb (400 mm × 200 mm) 3900 cells with a cylinder diameter of 6.3 mm could be built corresponding to 7800 corners of evolving hexagons. According to Karihaloo et al. (2013) in this scenario it takes 36.3 s to reduce the original radius R_0 of a cylinder to $r^*=1/3\ R_0$ at the corner of a rounded hexagon. They measured r^* at the thickened upper rim of the final rounded hexagonal cells, which is a methodological mistake. However, our Fig. 6 shows that the original radius is not reduced to 1/3 but to 1/8 to 1/10. From Fig. 4 of Karihaloo et al. (2013) one can read that in this case the time necessary to reach this radius is about 70 s. Therefore a total of about 450 hours would be required only for heating. The authors explain that their calculations are based on a two dimensional model and that "the constraint provided by the third dimension is likely to increase the time we have calculated". In other words: the working time of the bees needed for fusing the cylinders to hexagons for this one honeycomb is substantially more than 450 hours. Taking all this into account we can say that the time derived by Karihaloo et al. (2013) for the transformation of cylindrical tubes into hexagonal cells does not support the cylinder hypothesis, but proves it wrong.

At this point it should be noted that the claim that honeybees use their own body as a mould for the construction of the cells (Tautz, 2012, Tautz and Steen, 2017) cannot be valid for drone cells. For worker cells, a bee should be inside the cell during the construction and build the wax cylinder around itself (Tautz, 2012). Or other bees build the cylindrical cell around it. How that should work for short cells in the beginning of cell construction, is a mystery. In addition, the cross section of the bees' body is not really circular and has not the same diameter over the body length. It is not explained how a wax cylinder with a uniform diameter over its entire length is formed by using the bees' body as a mould. Moreover, not all individuals of a colony are of the same size. If the authors were right, the cell diameters of a honeycomb would also show this size distribution, which is not the case.

3.2.6 The uniform thickness of the cell walls cannot be generated by fusion of adjacent cell walls

The cell walls beneath the bulge on the upper rim show a uniform thickness of approximately 0.07 mm over the entire length, which is considerably thinner than directly at the rim (Fig. 6). Let us assume that the walls were formed by fusing two adjacent cylinders. At the corners of the hexagons where three adjacent cylinders would have merged according to the cylinder hypothesis, the wall should be 1.5 times thicker. But the bee-made cells in Fig. 6 do not show this. In pictures of Karihaloo et al. (2013), which are intended to make the cylinder hypothesis plausible, the walls are about twice as thick and the corners are formed of flat triangles. When comparing their Fig. 1a with 1b the question arises of where all the wax has remained during the transition to the hexagonal shape. Flowing of the wax would explain a small mass displacement to the cell corners, but not the disappearance of at least 50 % of the wax.

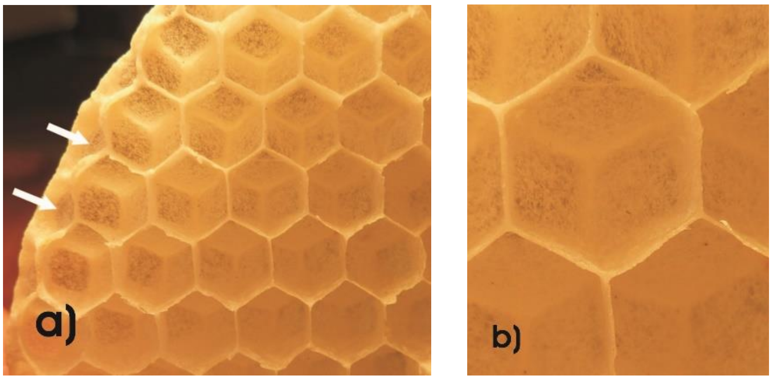

Fig. 6 Cross-section of cells, upper rim cut off; a) uniform thick cell walls of a natural honeycomb; on the edge rhombuses are already put on (arrows) which are completed during ongoing construction; b) detail of 6 a

3.2.7 The particular importance of the cell bottom (mid-wall) for the honeycomb construction

After completely removing the cell walls of a honeycomb, one can see that the corners of the cells on both sides of the comb are determined by the rhombic structure of the respective bottoms (Fig. 7). With the construction of the bottom the foundation of the honeycomb is laid down and it becomes evident that the plan of the cells is hereby fixed. Therein both the hexagonal shape of the cell and its lateral dimensions are already specified. It is hard to conceive that circular tubes are built on this hexagonal basis. According to Tautz (2012, p. 162) it is innate to the bees to stick wax lumps where wax already exists. The construction bees recognize “wax available” at the convex edges of the base structure as it is progressively built. It seems evident that on these wax lines the cell walls are pulled up directly in the hexagonal shape. This is supported by experiments with mid-walls cast to provoke the bees to build smaller brood cells (e. g. with 4.9 mm diameter) as a means of mite-control. Here too the bees build up the cells on the convex wax lines of this mid-wall with the smaller measure (Spiewok, 2014). Thus it is not so much to answer the question of how the bees build the regular hexagonal cells, but rather to ask how they manage to create the structure of the base, which contains the blueprint for the cells. The question of how bees build hexagonal cells is obviously the wrong one. The question should be: how do bees build their honeycombs? The consideration of the cells in isolation, without including the mid-wall, is misleading.

Fig. 7 After the cells are cut off, the view on the mid-wall of a natural comb shows that it contains the blueprint for the hexagonal cells

When constructing a comb, the bees stick wax lump to wax lump and so they build up the complete 3-d structure step by step. One can assume that honeybees build mid-walls and cells after the principles of modern 3d-printers.

3.3 Combs of wasps and hornets

Not only honeybees, but also the phylogenetically related wasps and hornets, build combs with hexagonal cells. However, they cannot produce their own building material, but they can make it by chewing rotten wood. The paper-like mass hardens and has no plastic properties. Thus the cylinder hypothesis fails to explain the construction principle of these species. This point was recently made by, amongst others, Oldroyd and Pratt (2015). Therefore it is reasonable to assume that no flow-assisted formation of the hexagonal cells takes place in the bees' honeycomb construction either. The protagonists of the cylinder hypothesis say that these species build "geometrically more generously" (Tautz, 2012, p. 167). Fig. 8 shows that this is not true. Bergmann and Ishay (2007) found that for Vespa orientalis the width of a single comb cell is about 10 mm and the basic symmetry of an entire comb of such cells is usually satisfied within absolute errors of no more than a few tenths of 1 mm. Wasps and hornets begin the construction of their nests with a vaulted roof, which corresponds in some way with the mid-wall of a honeybee comb. The common walls of the cells are constructed on the elevations on its underside. The arrangement of the curvatures which stabilize the construction (Mirtsch, 2011) reveals hexagonally close-packed structures (Fig. 8b). We can formulate that the combination of the two construction principles, (1) “hexagonal close-packing (space economy)” and (2) “adjacent cells, have a thin common wall (material economy)”, as in the case of honeybees, inevitably result in an assembly of cells with hexagonal cross-section without a planned action by the wasps or hornets. Hexagonal cells are therefore the consequence of the above-mentioned principles, not vice versa. It can therefore be assumed that comb construction with hexagonal cells was already established, even before honeybees and wasps diverged in their evolution about 100 million years ago.

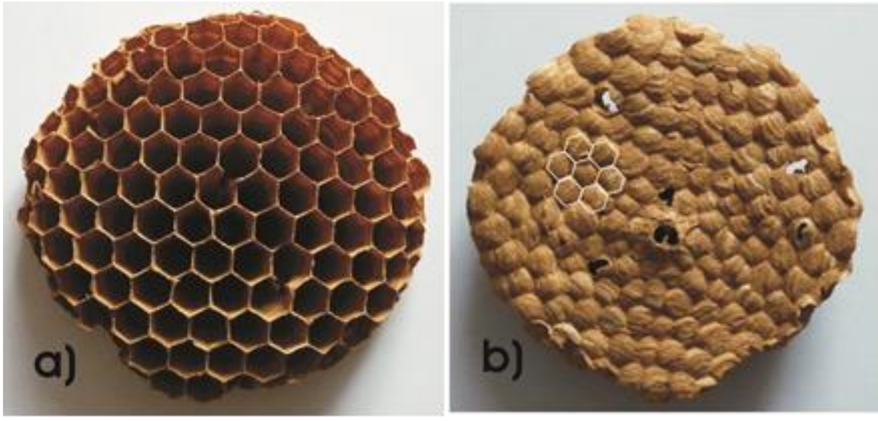

Fig. 8 Hornet’s comb with slight mechanical damage; a) hexagonal cells made of paper; b) back of the comb with convex vaults, hexagonal structures visible (white hexagons drawn). Courtesy of wasps-adviser Karl Lipp from Neuötting, Germany.

4 Conclusions

Based on scientific publications and our own considerations and observations, we show that the hypotheses of Pirk et al. (2004) concerning comb building of honey bees are not correct. Many constructive details of the honeycomb cannot be explained with them. The bees build mid-wall and hexagonal cells directly and without intermediate steps, in contrary to these authors who assume a construction of cylindrical tubes first. Furthermore bees are not able to build close-packed circular precursor cells. We proved experimentally that surface tension driven flow of the wax is irrelevant for comb building. The cylinder hypothesis would work only under the unreasonable condition that the wax is not only plastic, but liquid. Also self-organisation of the wax into hexagonal cells does not take place. Even in the model of Pirk et al. (2004) the formation of hexagonal cells by an increase of the temperature could only be called a “shape-transformation” without changing the existing hexagonal close-packed pattern of the circular cells. The high temperature needed for the fusing of the circular wax tubes cannot be generated by the bees. The calculations which should support the cylinder hypothesis prove the opposite according to our analysis. The construction of drone combs, under the assumptions of the cylinder hypothesis, would require an expenditure of co-ordination and time which could not be carried out by the bees. It is also very unlikely that the body of the bees serves as a mould for the wax cylinders.

The bottom of a cell is shaped of three congruent rhombi which are first of all formed during the construction at the edge of the honeycomb. We are convinced that the mid-wall contains the construction plan for the hexagonal cells, which are directly built on the convex wax lines of the rhombic structure. In order to obtain new insights into the comb building process, the three dimensional structure of the comb must be taken into account. This corresponds to the observable progress of the construction of new combs where the bees build small hexagonal cells at the comb rim. Also the so-called half-cells in “house-shape”, which connect the comb with the nest wall, prove that the cells are built directly without intermediate stages. These peripheral cells cannot be generated by the mechanism of the cylinder hypothesis.

To confirm our argumentation, we examined the rim of combs, the rear of a one-sided built comb, the onset of comb building, the mid-wall, cells with the upper rim cut off, heat treated wax samples and a hornet comb. We did not observe any wax-free voids on combs just under construction. They would be expected according to the cylinder hypothesis at the points where three tubes meet. We recognized that the mid-wall can be regarded as assembled of parts of the Plateau’s minimum plane of the regular tetrahedron. This confirms that not only the cells but also the mid-wall is built with minimal wax consumption in combination with extraordinary mechanical strength. We observe not only on combs of honeybees but also on combs of wasps and hornets two construction principles: (1) the cells are arranged in a hexagonal close-packed manner and (2) neighbouring cells are separated by a common thin wall. We state that the combination of these two construction principles will inevitably produce cells with hexagonal cross-section without intentional action of the bees, wasps or hornets.

We come to the following findings and conclusions:

a. Bees build the cells directly in hexagonal shape without any intermediate steps.

b. The building plan for the cells is established in the mid-wall.

c. The bees build the cell-walls directly on the convex wax lines of the structured mid-wall.

d. The three rhombi which form the cell bottom are built directly during the construction at the rim of the comb.

e. A flowing of the wax which could influence the cell geometry does not take place.

f. No detail of the honeycomb structure is produced by self-organization of the wax.

g. The hexagonal cross-section of the cells is generated by the combination of two building principles: hexagonal close-packing of the cells and adjacent cells share a common cell-wall.

h. The answer to the question in the title of Pirk et al. (2004) is NO.

Up to now, the question remains of how the tilt (up) of the long axis of the cells relative to the horizontal on both sides of the comb is made. This tilt against gravity is an additional argument against self-organization of the wax and thermoplastic flow in honeycomb construction.

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